Evidence of late migrant smolts of Atlantic salmon (*Salmo salar*) in the Loire-Allier System, France

by

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Abstract. – Smolts of Atlantic salmon *Salmo salar* of the Loire-Allier system have to perform an exceptional distance of 900 km to reach the ocean from the upstream spawning grounds, while being subjected to connectivity disruption induced by the presence of dams as well as fluctuating climatic conditions. In order to successfully perform their marine entry, smolts should reach the estuary within a limited suitable period. This study concerns smolt emigration dates from upper Allier, and arrival dates in the Estuary, as well as estimation by radio tracking of downstream migration speed. Comparison of these data revealed that a significant fraction of smolts from upper Allier leave breeding areas too late for successful marine entry. This delay may be partly induced by dam retention. We emphasize the importance of the clearing of the Poutès dam planed in 2015 and recommend to pursue and extend the current survey with additional monitoring stations along the migration axis, in order to study the fate of late migrants. These studies have major implications for the restoration of the threatened population of the Loire salmon.

Résumé. – Mise en évidence de smolts de saumon atlantique (*Salmo salar*) à migration tardive sur l'axe Loire-Allier, France.

Les smolts du saumon atlantique *Salmo salar* de l'axe Loire-Allier doivent parcourir une distance exceptionnelle de 900 km pour rejoindre l'océan depuis les zones de frayère amont, tout en étant soumis à des ruptures de connectivité induites par la présence d'aménagements ainsi qu'à des conditions climatiques fluctuantes. Afin de réussir leur passage en mer, les smolts doivent rejoindre l'estuaire dans une période favorable limitée. Cette étude porte sur les dates de migration des smolts en amont de l'Allier et de leur arrivée à l'estuaire, ainsi que sur l'estimation par radio pistage de la vitesse de migration. La confrontation de ces données révèle qu'une fraction significative des smolts du haut Allier quitterait trop tardivement les zones de reproduction amont du bassin versant pour réussir leur passage en mer, une partie de ce retard pouvant être liée à l'effet des retenues. Nous soulignons l'importance de l'effacement du barrage de Poutès prévu en 2015 et recommandons de poursuivre les suivis actuels et de les compléter par de nouvelles stations réparties le long de l'axe de migration afin d'étudier le devenir des migrants tardifs. Ces études ont des implications majeures pour la restauration de la population menacée du grand saumon de Loire.

Atlantic salmon (*Salmo salar* L.) is an anadromous species, which migrates long distances from reproduction areas in rivers to feeding areas in the sea and has already disappeared from most of the large European rivers. In France, a wild population subsists in the Loire catchment with reproduction areas mostly located in the upper part of its main tributary, the Allier (Thibault, 1994). The Loire-Allier River is the longest fresh water migration distance for Atlantic salmon in the northeast Atlantic region, with spawning areas located 920 km from the ocean. For smolts, the distance to reach the ocean from the spawning grounds is particularly long, and is bound to connectivity disruption induced by the presence of amenities (28 dams or barriers) as well as fluctuating and degraded environmental conditions.

The timing of a smolt arrival at the sea is crucial for its successful acclimatization and survival, and the favourable period for smolt marine entry is determined by the synchronization of two temporal windows (Boeuf *et al*., 1985; Berglund *et al*., 1992; McCormick *et al*., 1998). Firstly, smolts must reach the estuary in a good physiological condition to adapt successfully to salt water, and, afterward, to grow in the ocean. The period during which smolts are physiologically able to adapt to salt water and thus to succeed their marine entry is called the "physiological window". It is related to the activity level of the gill NaKATPase (McCormick *et al*., 2003) and is limited to a few weeks (Boeuf *et al*., 1985; Berglund *et al*., 1992; McCormick *et al*., 1998). Secondly, smolts must reach the estuary under favourable environmental conditions encountered during a period called the "environmental window". After this period, in summer, there is

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an increased probability to encounter unfavourable environmental conditions such as high temperature, low dissolved oxygen concentrations, predators, or pollution (Hvidsten *et al*., 1998; McCormick *et al*., 1998; Antonsson and Gudjonsson, 2002; Jutila *et al*., 2003; Jutila *et al*., 2005). Thus, some late migrating smolts may wait for the subsequent autumn, winter or spring, for their marine entry (Youngson *et al*., 1983; Riley *et al*., 2008) but this delay would have consequences on their survival (Hansen and Jonsson, 1989), as well as on their ability to imprint the location of their home river (Hansen and Jonsson, 1991). This timing of a smolt's arrival at the sea can be expected to be of greater importance in very long river systems, where climatic and anthropogenic conditions have the potential to considerably delay downstream migration (McCormick *et al*., 2003). In this context, we hypothesize that the current salmon population on the Loire-Allier may not be adapted to such drastic conditions. The late migrant smolts might not reach the estuary on time to succeed their marine entry.

Our study, aimed at providing a first investigation on the timing of the downstream migration of smolts of the upper Allier in order to 1) provide and synthesize available data on smolt downstream migration of the Loire-Allier system, 2) evaluate the compatibility of the smolt emigration dates from the upper part of the Allier with the passage in the estuary, and to test the existence of late migrants, 3) point out important research lines which should be investigated on the Loire-Allier system in the near future.

MATERIAL AND METHODS

Study area

The Loire catchment occupies more than one-fifth of the land area of France with an area of 117 000 km^2 (Fig. 1). The Allier is the main direct tributary of the Loire and the upper Allier has been historically known as the most functional spawning zones for Atlantic salmon. After draining a 14 310 km^2 catchment area parallel to the upper Loire in 421 km long, the Allier flows into the Loire at the Bec d'Allier located 568 km from the ocean (pk = 568 km) (pk = distance from the ocean). Since 2008, a "refuge area" without stocking was set up on the Allier from its source to upstream Chanteuges (pk = 863 km) (Fig. 1).

Smolt recording

Poutès Dam (pk = 890 km)

The hydroelectric complex Poutès-Monistrol, called hereafter "Poutès dam", is located 890 km from the ocean (WGS84 coordinates: 3°40'22.92''E 44°56'49.61''N), (Fig. 1). It was built in 1943, has a length of 70 m, a height of 17 m and creates a 3.5 km long reservoir of 2.4 million m^3. In order to allow the downstream migration of smolts, a slider device was built in 1985; it was put into service each year from March 15 to June 15 (Tab. I) and was fed continuously by a flow of 2.5 m^3/s. All fish crossing the dam through the slider are video-recorded. The counting of video recorded smolts was made on daily basis by Logrami association for Électricité De France. Data from 2009 to 2011 are provided. The current limits of this system are the starting date (March 15) due to too drastic climatic conditions earlier

Table I. - Smolt number migrating from the Poutès dam, France (pk = 890 km).

Year	Monitoring period	Period of smolt presence on record	Smolt number
2009	Mar. 16-Jun. 15	Mar. 20-Jun. 15	319
2010	Mar. 16-Jun. 15	Mar. 16-Jun. 13	1976
2011	Mar. 15-Jun. 15	Mar. 15-Jun. 12	262

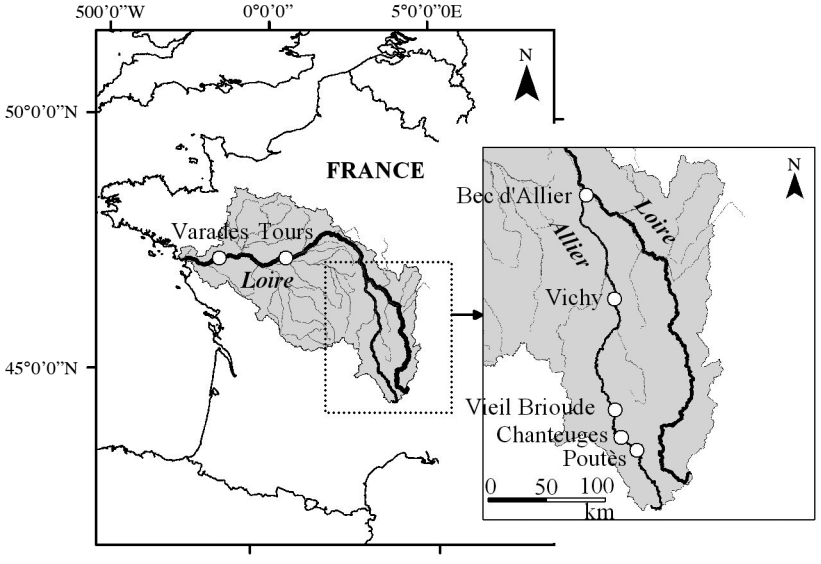

Figure 1. - Study area.

Table II. - Number of smolts caught at Chanteuges, France (pk = 863 km).

Year	Capture period	Interruption period	Period of smolt presence on catch	Smolt number	Mean body length (mm)	Mean body weight (g)
2009	Mar. 17-May 31	Mar. 18-30 Apr. 11-28	Mar. 17-May 26	196	155 ± 19	31 ± 11
2010	Mar. 17-May 31	Mar. 27-29 May 11-21	Mar. 18-May 31	479	152 ± 23	30 ± 15
2011	Mar. 15- May 27	Mar. 15-19	Mar. 15-May 27	133	156 ± 23	34 ± 15

Table III. - Rotary trap efficiency at Chanteuges, France (pk = 863 km).

Year	Type of mark	Smolt origin	Upstream released smolt number	Recaptured smolt number	Trap efficiency
2009	Adipose fin removal	Hatchery	200	9	4.50%
	Caudal fin mark	Wild	123	7	5.70%
2010	Adipose fin removal	Hatchery	125	5	4.00%
	Caudal fin mark	Wild	42	2	4.80%
Total			490	23	4.70%

Table IV. - Number of smolts caught at Varades, France (pk = 132 km).

Year	Capture period	Capture event number	Period of smolt presence on catch	Smolt number	Mean body length (mm)	Mean body weight (g)
2009	Mar. 31-Jun. 9	22	Apr. 8-May 25	66	175.9 ± 16.6	46.6 ± 16.6
2010	Mar. 27-May 31	22	Mar. 31-May 19	116	171.4 ± 17.4	41.3 ± 13.6
2011	Mar. 23-Jun. 7	20	Mar. 31-May 16	24	179 ± 16.4	44.1 ± 13.5

in the year; and the fact that some smolts may be out of view during floods (Bach *et al*., 2011a).

Chanteuges rotary trap (pk = 863 km)

Description

Catches of smolts were made by the Conservatoire National Saumon Sauvage (CNSS) with a rotary screw trap located in Chanteuges (pk = 863 km) (WGS84 coordinates: 3°32'1.63''E 45°4'45.59''N), (Fig. 1) in order to control the smolts emigrating from the upper Allier. The rotary screw trap device (EG Solutions, Inc., Corvallis, Oregon, US) was successfully used in previous studies of smolt downstream migration (Sykes *et al*., 2009; Music *et al*., 2010; Riley *et al*., 2010). The device and utilisation of the rotating smolt trap (1.52-m orifice) has been thoroughly described (Thedinga *et al*., 1994). In 2009, 2010 and 2011, the trap was continuously deployed from March to June, except when the flow rate was higher than 60 m^3.s, which is more than twice the annual mean flow. These conditions caused two interruption periods in 2009 (18-30 March and 11-28 April) and in 2010 (27-29 March and 11-21 May), and one interruption period in 2011 (15-19 March) (Tab. II).

The presence of salmon smolts in the trap was checked once a day. Regular cleaning was performed to prevent clogging of the rotary trap, which could reduce its efficiency. When present in the trap, the individuals were caught and anesthetized individually. Body length and weight were measured and apparent health status was checked. Smolts were then placed in a recovery tank before being released or preserved in CNSS if used for breeding.

Capture efficiency

The rotary trap efficiency was determined on both hatchery and wild smolts in 2009 and 2010. Hatchery smolts were marked by adipose fin removal and released 1 km upstream the rotary trap site. Wild smolts were trapped in the rotary trap and marked with a caudal fin mark. Then, they were also released 1 km upstream the trap site, and thus they were available for recapture a second time in the trap (Tab. III). The percentage of the marked fish recaptured was used to estimate trap efficiency (Seelbach *et al*., 1985).

Varades (pk = 132 km)

In the downstream part of the Loire, at the entry of the Estuary, smolt sampling was carried out by a professional fisherman using a trap called a "guideau" initially designed for catching downstream migratory eels. The frame used for this study is a funnel-shaped net 22 m long, 9 m wide and 4.5 m high. Catches were located in the Loire on the town of Varades (pk = 132 km) (WGS84 coordinates: 1°1'45.94''E 47°23'5.69''N), (Fig. 1), where the width of the Loire was about one hundred meters. Catches were performed from 2009 to 2011, during 20 to 22 nights (10:00 p.m. to 6:00 a.m.) each year between the end of March and the beginning of June (Tab. IV). Smolt body length and weight were measured and their apparent health status was checked. Then the fishes were released.

Downstream migration speed

Two radio-tracking studies were performed in 2005 and 2006 to estimate the speed of downstream migration. These studies covered most of the system (544 km) from

the upstream basin of the Allier in Vieil Brioude (pk = 823 km) to Tours (pk = 279 km) (Fig. 1).

Radio tracking material

The radio-tagged smolts were F1 smolts (wild parents) produced at the CNSS. A total of 58 smolts were tagged, separated into 4 batches, depending on the release date (2005, March 25 and April 12; 2006, May 12 and May 19) and location (Vieil Brioude pk = 823 km or Vichy pk = 674 km). Smolts were individually anesthetized. Then a transmitter was gently pushed from the mouth to the stomach cavity using a tube. Tagged fish were placed in an oxygenated recovery tank for 48 to 96 hours and were released. The equipment used for the study was supplied by the U.S. company Advanced Telemetry Systems, ATS. The radio transmitters used were ATS F1440 (weight: 2,1g, life: 60 days) in 2005 and ATS F1430 (weight: 1.7g, life: 36 days) in 2006. The tag to body weight ratio was less than 4%.

Receiver positions

In 2005, two receivers with recorders were first installed at the Vichy's dam (pk = 674 km) and downstream of the Wilson Bridge in Tours (Université François-Rabelais, pk = 279 km) (Fig. 1). When the second batch was released downstream of the Vichy dam, one receiver initially installed at Vichy was moved further downstream at the dam des Lorrains, located at Bec d'Allier (pk = 568 km). In 2006, two receivers with recorders were installed at the dam des Lorrains and downstream of the Wilson Bridge in Tours. In addition in 2006, a manual receiver-recorder was used at Vichy at an almost daily basis.

Migration speed

Migration speed was calculated by dividing the distance between receivers by the time need by the smolt to travel the distance (Tab. V).

Table V. - Smolt migration speed estimated by radio tracking. Mean value: 32.2 ± 19.2 [8.25-106] km/day.

Batch	Release date	Smolt number	Mean weight	Mean total length	Release location (pk in km)	Reception date	Smolt number	Recapture location (km from ocan)	Traveled distance (km)	Mean speed (km/day)
Batch 1	25 Mar. 2005	14	76.0 g (± 15.2)	204 mm (± 14)	Vieil-Brioude (823)	29 Mar. 2005	1	Breuil-sur-Couze (790)	33	8.25
						29 Mar. 2005	1	Vichy (674)	149	37.25
						31 Mar. 2005	1	Vichy (674)	149	24.83
						6 Apr. 2005	3	Vichy (674)	149	12.42
						12 Apr. 2005	1	Tours (279)	544	30.22
						18 Apr. 2005	1	Downstream Tours (261)	562	23.42
Batch 2	12 Apr. 2005	14			Vichy (674)	13 Apr. 2005	1	Bec d'Allier (568)	106	106.00
						16 Apr. 2005	5	Bec d'Allier (568)	106	26.50
						18 Apr. 2005	1	Upstream Tours (292)	382	63.67
						18 Apr. 2005	1	Bec d'Allier (568)	106	17.67
						19 Apr. 2005	1	Tours (279)	395	56.43
						20 Apr. 2005	1	Tours (279)	395	49.38
						24 Apr. 2005	1	Tours (279)	395	32.92
Batch 3	12 May 2006	15	56.5 g (± 6.8)	180 mm (± 10)	Vieil-Brioude (823)	17 May 2006	1	Vichy (674)	149	29.80
						18 May 2006	1	Bec d'Allier (568)	255	42.50
						22 May 2006	1	Bec d'Allier (568)	255	25.50
						1 Jun. 2006	1	Tours (279)	544	27.20
Batch 4	19 May 2006	15			Vieil-Brioude (823)	23 May 2006	1	Vichy (674)	149	37.25
						24 May 2006	1	Bec d'Allier (568)	255	5.00
						26 May 2006	2	Vichy (674)	149	21.29
						26 May 2006	2	Bec d'Allier (568)	255	36.43
						28 May 2006	1	Vichy (674)	149	16.56
						29 May 2006	1	Bec d'Allier (568)	255	25.50

Estimation of late migrant percentage

Period of smolt marine entry

The median observation date, which corresponds to the date of the year when half of the smolt have been captured in Varades, was used to estimate the timing of the smolt marine entry.

Comparison of migration dates along the Loire-Allier system

The median observation dates were similarly calculated for the emigration dates from upper Allier locations (Poutès and Chanteuges). Direct comparison between these emigration dates and the marine entry date (see above) was performed taking into account the average downstream migration speed (see above). Discrepancies between these dates allowed to providing a first estimation of the occurrence of late emigration timing from upper Allier.

Late migrant percentage

A complementary approach was used to evaluate the proportion of late migrants from the smolt population of upper Allier and estimate the ultimate emigration date to reach the estuary for marine entry under suitable conditions. For this preliminary study we considered that the physiological window to succeed the marine entry is limited only to a couple of weeks (Boeuf *et al*., 1985; Berglund *et al*., 1992; McCormick *et al*., 1998). The end of the suitable period of marine entry was arbitrary fixed as 3 weeks (21 days) after the median observation dates in Varades. Within the smolt population of the upper Allier (i.e. Poutès and Chanteuges), the percentage of late migrant individuals was estimated per year, following these four steps:

(i) Estimation of the period of smolt marine entry (data from Varades);

(ii) Estimation of the time necessary to reach the sea from the upper Allier, based on the downstream migration speed estimation;

(iii) Estimation of the limit date of departure from the upper Allier to reach the sea during the suitable period for marine entry;

(iv) Per year, estimation of the percentage of smolts from the upper Allier that could arrive to the sea within the suitable period of smolt marine entry; and, conversely, the percentage of the smolts that could be considered as late migrants.

RESULTS

Smolt recording

Poutès Dam

From March 15 to June 15, a total number of 318, 1976 and 199 smolts were recorded in 2009, 2010 and 2011, respectively (Tab. I, Fig. 2). Median migration dates were May 01, April 24 and April 23 in 2009, 2010 and 2011, respectively (Tab. VI, Fig. 3).

Chanteuges rotary trap

Capture efficiency

At Chanteuges a total of 490 smolts have been marked and released 1 km upstream in 2009 and 2010, among which 23 individuals have been recaptured (Tab. III). Average trap efficiency was around 5%, for both wild and hatchery smolts (5.5 and 4.3%, respectively).

Smolt catches

From March 15 to May 31 a total of 196, 479 and 133 smolts were caught in 2009, 2010 and 2011, respectively (Tab. II, Fig. 2). Median migration dates were April 4, April 19 and March 15 in 2009, 2010 and 2011, respectively (Tab. VI, Fig. 3). Smolts were all in good condition and showed no injury.

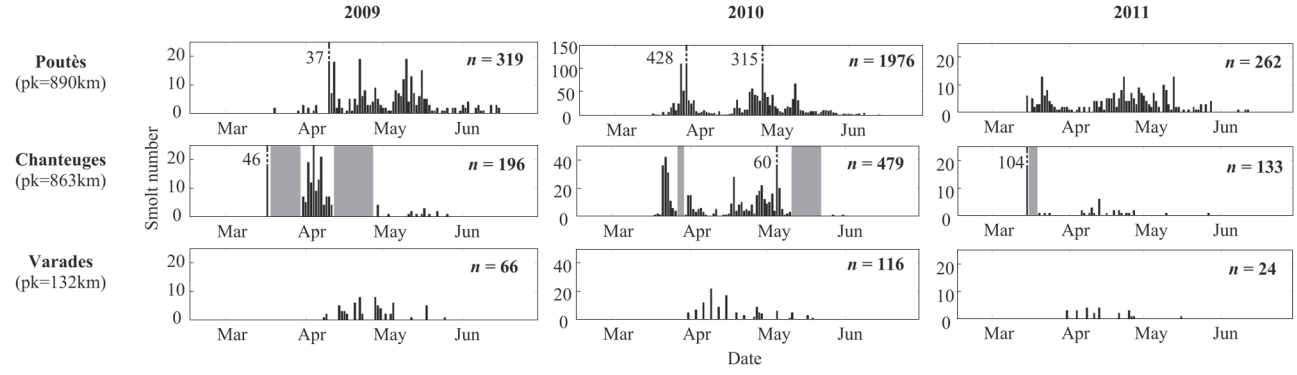

Figure 2. - Smolt number observed in Poutès (pk = 890 km), Chanteuges (pk = 863 km) and Varades (pk = 132 km) in 2009, 2010 and 2011. Grey area represents period of no catch (see text for details).

Table VI. - The timing of the smolt migration was estimated annually by the date when half of the total smolt catches had occurred (median observation date) in Poutès (pk = 860 km), Chanteuges (pk = 863 km) and Varades (pk = 132 km).

Location (pk in km)	2009	2010	2011
Poutès (890)	May 01	Apr. 24	Apr. 23
Chanteuges (863)	Apr. 04	Apr. 19	Mar. 15
Varades (132)	Apr. 28	Apr. 15	Apr. 11

Varades

Smolts reaching the estuary at Varades were caught every year from March 31 to May 31 for fishing periods covering March 27 to June 30. A total of 66, 116 and 24 smolts were captured in 2009, 2010 and 2011, respectively (Tab. IV, Fig. 2). Median migration dates were April 28, April 15 and April 11 in 2009, 2010 and 2011, respectively (Tab. VI).

Downstream migration speed estimation

The mean value of the smolt migration speed estimated by radio-tracking was 32 ± 19 km/day (n = 31 smolts successfully recorded) (Tab. V). Among them, 7 smolts had covered a distance longer than 300 km. They were recorded on downstream area, after travelling from 382 to 562 km. Their mean migration speed was 40 ± 16 km/day (Tab. V).

Estimation of late migrant smolts

Comparison of migration dates along the Loire-Allier system

Direct comparison between median emigration dates from upper Allier (Poutès and Chanteuges) and median date of arrival at the estuary (Varades) indicated several discrepancies (Tab. VI). First, comparison between the two sites at the upper Allier showed that the median emigration date in Poutès (pk = 890 km) was each year later than in Chanteuges (pk = 863 km): May 01/April 4 in 2009, April 24/April 19 in 2010, April 23/March 15 in 2011. Second, comparison between upper Allier (Poutès and Chanteuges) and the Loire Estuary (Varades, pk = 132 km) showed that the median emigration date in Poutès (pk = 890 km) was each year later than in Varades: May 01/April 28 in 2009, April 24/April 15 in 2010, April 23/April 11 in 2011. For Chanteuges, median emigration date was earlier than in Varades in 2009 (April 4/April 28) and 2011 (March 15/April 11) but later in 2010 (April 19/April 15). Considering the distance between Chanteuges and Varades (731 km) and the average smolt downstream migration speed (32km/day), the smolt would need 22 days to migrate from Chanteuges to Varades. This is compatible with the migration dates in 2009 and 2011. These comparisons indicate that median emigration dates of smolts from upper Allier were late every year in Poutès and in 2010 in Chanteuges.

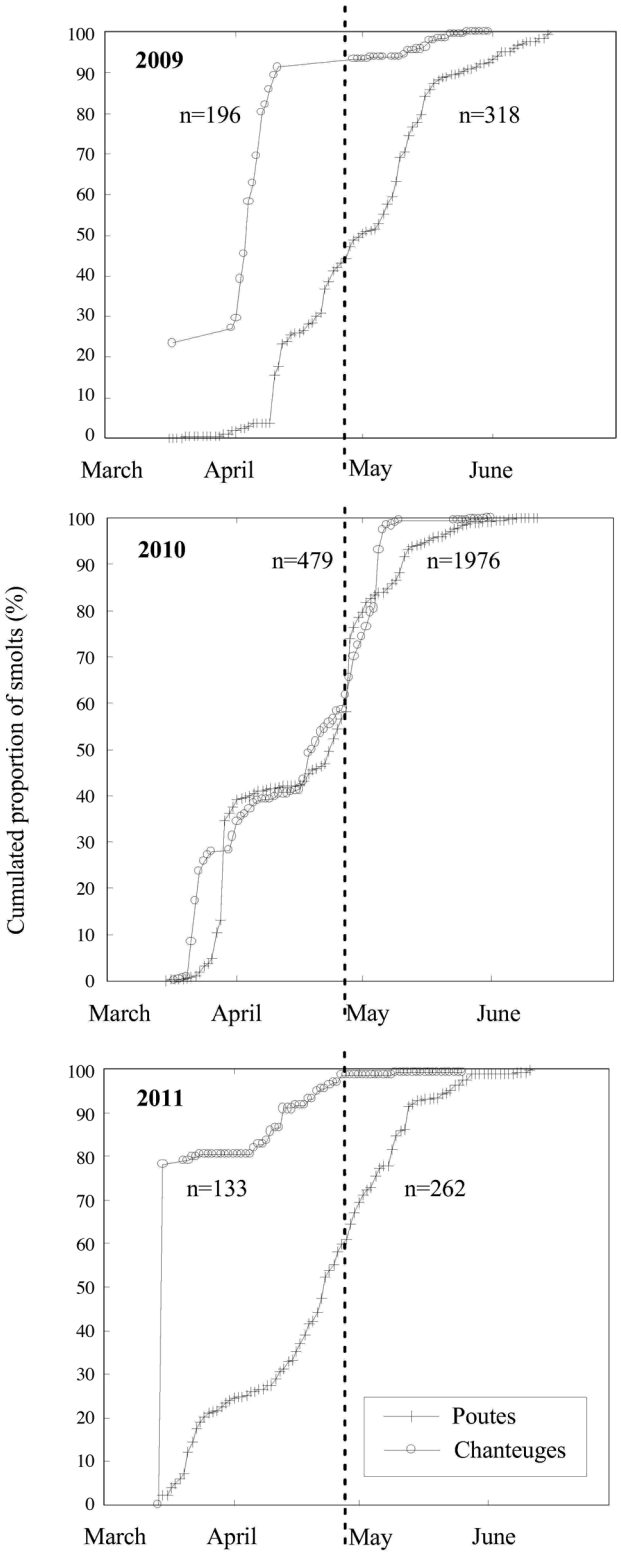

Figure 3. - Cumulated proportion of smolts migrating from Poutès (pk = 890 km) and Chanteuges (pk = 863 km) in 2009, 2010 and 2011. Striped line represents the deadline (April 26: see text for details) of smolt emigration from the upper Allier to reach the estuary during the suitable period of marine entry.

Estimation of late migrant percentage

The timing of the smolt arrival in estuary was characterized annually in Varades by the median observation date (April 28 in 2009, April 15 in 2010, and April 11 in 2011; Tab. VI). Mean date was April 18. The end of the suitable period of marine entry was arbitrary fixed to be three weeks later on May 10. Considering the distance and smolt downstream migration speed, smolts should emigrate from the upper Allier (Poutès and Chanteuges) before April 26 in order to reach estuary under favourable conditions (before May 10). Conversely, smolts emigrating from Poutès and Chanteuges after April 26 could be considered as late migrants. Based on this calculation, 55% of smolts emigrating from Poutès and less than 10% of smolts emigrating from Chanteuges could be considered as late migrants in 2009 (Fig. 3). In 2010, 40% of smolts emigrating from both Poutès and Chanteuges could be considered as late migrants. In 2011, 40% of smolts emigrating from Poutès and less than 2% from Chanteuges could be considered as late migrants (Fig. 3).

DISCUSSION

The present study on the downstream migration of smolts of the Loire-Alier system provides the first comparison of migration dates between the upper Allier and the Estuary, revealing the occurrence of late migrants from upper Allier.

Data reliability

This study is based on three year data from video recording of smolts at Poutès dam (pk = 890 km) and from catches of smolts at Chanteuges (pk = 863 km) and at Varades (pk = 132 km). In the upper Allier, we are aware that the data reliability are affected by high flows. During high flow periods, smolts can escape through the Poutès dam gates and the rotary trap cannot be used in Chanteuges (see material and methods). This limitation may particularly biases the dataset since it has been shown that the waves of migration of smolts are linked to increased flow (Hvidsten *et al*., 1995; Sykes *et al*., 2009). In Varades, an increase in the number of fishing dates could be recommended for future studies to further characterize the period of smolt arrival in the Estuary. The efficiency of the rotary trap in Chanteuges has been evaluated at 5% using both wild and hatchery smolts. We advise that similar studies should be performed to evaluate the efficiency of the measures at Poutès and at Varades. The expertise of the available data revealed a lack of information distributed all along the Loire-Allier system of migration. To improve the understanding of the smolt migration process, additional data are needed, especially on intermediate positions along the axis of migration.

Inter-annual variability in smolt number

Inter-annual variability in the number of recorded smolts was observed for all the three sites, with the maximum smolt numbers observed in 2010 and the minimum in 2011. Variation in smolt number depends primarily on the abundance of salmon that spawned the previous years. For instance, the number of spawners was shown to fluctuate with a ratio from 1 to 10 between 2006 and 2009 in the Allier (Bach *et al*., 2011b). Similar variations could explain the differences in smolt number observed in our study between 2009 and 2011. Annual variability in smolt number may also be linked to the variations of climatic and hydrometric conditions. Very low spring flows and high temperatures (Bach *et al*., 2011b) were likely detrimental to the smolt migration in 2011.

Migration delay in Poutès

Comparison of smolt median emigration dates in Poutès dam and Chanteuges showed that the emigration was consistently later in Poutès than in Chanteuges, while Chanteuges is located 27 km downstream of Poutès. This paradoxical discrepancy reveals a striking delay in the emigration timing of the smolts located upstream of the Poutès dam. These differences in migration timing between Poutès and Chanteuges could have two complementary explanations:

(i) The delay of smolt migration in Poutès was likely induced by the physical blocking of smolts at Poutès dam, although some smolts were able to cross the dam without being recorded (Bach *et al*., 2011a);

(ii) A difference in temperature between these two sites of the upper Allier (2°C, Hélène Imbert *et al*., unpubl. data). As temperature is a key-factor for initiating smolt downstream migration (Jonsson and Ruud-Hansen, 1985; Zydlewski *et al*., 2005), colder temperature may delay the triggering of migration above Poutès. Early migrant smolts, originating from spawning areas located downstream Poutès, could thus partially explain the difference in smolt migration timing between Chanteuges and Poutès.

Estimation of smolt marine entry date

During the three years of sampling, 75% of smolt movements in Varades were observed before May 2, with a median on April 18. Our data are consistent with the historical passages of smolt in the Loire estuary. A recent model, SALSEA-Merge, generated by the Institute of Marine Research in Norway, allowed to estimate the date of smolt marine entry, based on the dates of capture of post-smolts on feeding areas at sea, and on genetic identification of the smolt origin (For more information: http://www.nasco.int/sas/salseamerge.htm). This model estimated the marine entry of smolts identified as originating from the Loire-Allier system to be April 20. This date is in complete agreement with our estimation of the median date of April 18 in Varades. This observed period of smolt marine entry likely represents the

favourable period for successful adaptation to saltwater and performance of the growth phase at sea. These smolts will consequently be participating in the recruitment of prospective spawners.

A direct comparison between the date of marine entry, the dates of emigration from upper Allier and the speed of smolt downstream migration, allowed us to reveal discrepancies and to provide a first estimation of the occurrence of late migrants (see below).

In a complementary approach, we considered a deadline for the suitable period of marine entry, taking into account the problems of the short "physiological window" and of the critical "environmental window" to evaluate the proportion and the fate of late migrants. In this calculation, we selected a broad amplitude of 3 weeks from April 18 to May 10, although the date of May 10 is arbitrary and should be used with caution. The designation of a fixed deadline as limit of the suitable period is criticisable but necessary to provide a preliminary evaluation of the late migrant proportion in the upper Allier. Future studies should focus on smolt recording in the Estuary and at sea to raise more information on this suitable period.

Smolt downstream migration speed

Radio tracking experiments were performed between upstream (Vieil Brioude, pk = 823 km) and downstream (Tours, pk = 279 km) sites of the Loire-Allier, in order to estimate the downstream migration speed. The mean speed value of 32 ± 19 km/day is in agreement with earlier reports, including mark recapture studies, made between Vieil Brioude and Saint Laurent des Eaux (Cuinat *et al*., 1975; Nihouaran A., 1976) and a radio tracking of one smolt in the Allier (Bach *et al*., 2008). From the present speed data, we estimate that smolts emigrating from upper Allier (Poutès/Chanteuges) will need an average of 22 days to reach the entrance of the Estuary (Varades).

Occurrence of late migrants from upper Allier

In Poutès, the median emigration date was every year later than the median arrival date in Varades, highlighting a major occurrence of smolt late migrants. In Chanteuges, the situation was similar than in Poutès in 2010, while in 2009 and 2011 the median emigration dates in Chanteuges were earlier than the respective median arrival dates in Varades. Furthermore, considering that the smolt would need 22 days to migrate from Chanteuges to Varades, migration dates in both sites are fully compatible in 2009 and 2011. We further analysed the late migrant occurrence by taking into account the deadline of the suitable period of marine entry. Based on this calculation, 40 to 55% of smolts emigrating from Poutès from 2009 to 2011could be considered as too late migrants. This proportion is more variable in Chanteuges, between less than 2% and 40% according to the year.

Our results reveal the existence of late migration within the upper Allier smolt population. A significant fraction of smolts from upper Allier may leave upstream breeding areas too late for a successful transition at sea. The inherent limits of our dataset make it difficult to accurately quantify this fraction within the smolt population. However, the existence of late migrants within the smolt upper Allier population cannot be questioned. As described by Marschall *et al*. *(*2011), temperatures downstream can reach lethal or near-lethal temperatures while smolts are delayed by dams. As a result, the match between the completion of migration and the window of appropriate migration conditions can be disrupted.

Fate of the late migrants

The existence of late migration within the upper Allier smolt population raises the question of the future of the individuals that cannot reach the ocean. Do they develop adaptive response and perform a two-year migration, and find locations of summer halt until the next year? It has been observed that Atlantic salmon juveniles exhibit differential patterns of migration during their life history. For example, a portion of the parr population migrates downstream in the autumn (Pinder *et al*., 2007; Riley *et al*., 2008; Ibbotson *et al*., 2011). Baisez *et al*. (2011) observed that salmon were forced to halt their migration during summer periods in the Loire-Allier when water temperatures were high. These observations were focused on adult upstream migration but we assume that this phenomenon may occur equally on late smolt migrants since inhibition of downstream swimming behaviour by elevated temperature has been shown on hatchery-reared smolts (Martin *et al*., 2012). The present study underlines the importance of protecting smolts, as well as their functional habitat, particularly in the locations of potential halt.

Perspectives

To conclude, we recommend continuing and extending the current survey of smolt migration on both the upper Allier and downstream on the Loire. We also highlight the necessity to develop additional indicators along the Loire-Allier system with the possible creation of new monitoring stations. The acquisition of complementary data on the intermediate Loire-Allier system will allow understanding the dynamics of migration, investigating the fate of late migrant smolts, and identifying possible areas of refuge.

We emphasize the importance of the clearing of the Poutès dam that has been planned for 2015. We recommend the initiation of a pluri-annual survey based on a tagging program of smolts upstream Poutès in order to follow the fate of late smolts and evaluate the effect of the Poutès dam clearing on smolt late migration. The proportion of late migrants within the population is expected to be strongly reduced, as

well as the duration of the migration. This study would also clarify the potential impact of cold temperature above Poutès on the migration. Because there are many other obstacles, in addition to Poutès, on the Loire-Allier system, we urge a survey with radio tracking from Poutès to Vichy that will assess the impact of the successive physical barriers on smolt downstream migration. Finally, we fully support the recommendation of assessing the gain of functional habitats, which would be induced by the connectivity restoration (Baglinière *et al*., 2005). The results will have significant implications for the choice of date and place of resettlement and will strongly contribute to the restoration of large individuals of this threatened species.

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